The effect of the faint fog in increasing the value of [V] = [W] is plainly seen in the morning observations. The effect also of a very few faint fleecy clouds is seen in the increase of [V] and of [U] for the observations at $1^h\ 0^m$ and $1^h\ 30^m$, before which no clouds had been visible. The air was saturated the whole day.

The candles which I used in all these observations, were the "Belmont Sperm," supplied to me so as to burn 100 grs. in 47 minutes.

"On the Minute Structure of the Muscle-Columns or Sarcostyles which form the Wing-Muscles of Insects. Preliminary Note." By E. A. Schäfer, F.R.S. Received December 15, 1890,—Read January 8, 1891.

[Plates 4 & 5.]

The fibres of the wing-muscles of most insects are made up of readily separable longitudinal elements, which are often called the "wing-fibrils," although several observers have remarked the existence of an apparently fine fibrillation in them. To avoid ambiguity, I shall employ the term "muscle-columns" (*Muskel-säulchen*, Kölliker), or its equivalent "sarcostyles,"* to designate these elements. They are united together to form the fibres by a not inconsiderable amount of granular interstitial substance (*sarcoplasm*, Rollett). This substance has been regarded (Ramón y Cajal) as the true contractile material of the muscles, but it is easy, nevertheless, to observe the contraction of the sarcostyles, isolated in white of egg, a fact which has been pointed out by more than one writer on the subject (Merkel, Kölliker).

If an insect of which the wing-muscles are of the character above described is cut open and placed in alcohol of about 90 p.c. for twenty-four hours or more, and is afterwards transferred to glycerine, the sarcostyles of the wing-muscles can be isolated and examined without difficulty; they exhibit almost every phase of extension and retraction (or contraction), and the usual appearance of alternate dark and light transverse bands, with a fine line traversing each light band. When stained with dyes, such as hæmatoxylin, the dark bands are found to take the staining most intensely; the fine transverse lines are much less stained, and the clear bands hardly at all. The various parts of the sarcostyle evidently differ from one another in their behaviour to staining reagents, and the transverse striation is not to be explained by the effect of the varicosities of the sarcostyle upon the light transmitted

* Σάρξ, flesh, στύλος, a column.

through it (Haycraft); moreover, many of the sarcostyles show no such varicosities. A more valuable, because more sharply selective, method of staining is that recommended by Rollett ('Wien. Akad. Denkschr.,' vol. 51) for alcohol-glycerine muscles. This consists simply in the after-application of the gold-formic method to the tissue. In place of treating the *fresh* muscle with chloride of gold and afterwards with formic acid, the *alcohol* muscle, which has been afterwards steeped in glycerine, is taken. If *fresh* muscles are thus treated, the sarcoplasm alone is stained, the sarcostyles remaining colourless (or they may be entirely dissolved by the action of the formic acid). In this way, in the leg-muscles, the often-described appearance of a network is obtained. But if the *alcohol-glycerine* muscle be taken, the reduction of the metal takes place *in the sarcostyles*, and almost exclusively in their dark bands, so that, while the interstitial sarcoplasm and the clear bands of the sarcostyles remain clear and colourless, the dark bands of the sarcostyles are deeply coloured of a tint varying from an intense purple-red to a faint purple-blue. Rollett recommends the application of this method to the study of the structure of the leg-muscles, but it is still better applicable to that of the wing-muscles, since it brings out in them, with a clearness which renders the application of the photographic method comparatively easy, points of structure which, up to the present, with the usual methods of investigation, have remained obscure.

Before describing the special points which are thus capable of elucidation, it is necessary to adopt names for the several parts of the sarcostyle. For the more or less cylindrical disk which forms the dark band I shall retain the name "sarcous element," without thereby intending to imply that it accurately corresponds to the part to which that name was originally applied by Bowman; in a general sense, I believe that it will be found to do so. The term represents, on the whole, the *Querscheibe* of the German, the *disque épais* of French, authors. The fine line which bisects the light band I shall term "transverse membrane" (*Quermembran*, Krause; *Zwischenscheibe* of German authors; *disque mince* of French writers). The light space separating the ends of the sarcous elements from the transverse membranes may, for the present, be simply spoken of as the "clear interval;" it corresponds with the isotropous substance of authors. The segment of a sarcostyle comprised between two transverse membranes may be termed "muscle-segment" or "sarcomere" (*Muskelkästchen*, Krause).

The relative amount of the sarcomere occupied by its several parts varies with the degree of extension or retraction (? contraction) of the tissue. In the retracted condition (figs. 1 and 1*a*) the sarcostyle, which is relatively thick and moniliform, appears formed almost

entirely of the sarcous elements, which are distinctly bulged, and are arranged closely succeeding one another with but narrow clear intervals between them. In these very narrow clear intervals the laterally-stretched and thinned-out transverse membranes cannot be seen unless the sarcous elements are forcibly dragged somewhat apart in the process of isolating them; if this is done the transverse membranes become visible (figs. 2 and 2*a*). In moderately extended sarcostyles (fig. 5) the sarcous elements are more separated from one another, the clear intervals being correspondingly longer and the transverse membranes distinct. In greatly extended sarcostyles (figs. 3 and 3*a*) the sarcous elements are not only lengthened and much narrowed, but show a tendency to separate in the middle into two halves, leaving a space between them. The clear intervals are also lengthened, and the transverse membranes are thickened; the whole sarcostyle being narrowed. It may be inferred, from the separation of the sarcous element, that it is really constituted of two halves, which in the retracted fibre abut against one another in the middle of the muscle segment, but in the extended fibre are separated from one another. Indications of this separation can be made out even in the non-extended sarcous element, as in some of those represented in fig. 8. Whether or not there is a fine membrane between the two halves, as described by Hensen, my preparations do not enable me to determine. Nor have I been able to observe in them the further separation, with still further extension, of separate disks (accessory disks, *Nebenscheiben*) from the ends of the sarcous elements, a separation which has been described and figured by several good observers.

In the preceding statements and descriptions there is nothing that is altogether novel or that has not been described with sufficient clearness by previous authors. But the application of photography leaves no room whatever to doubt the accuracy of those descriptions.

There is, however, one essential point of structure which I have only seen clearly in preparations made by this method, and which is also distinctly shown in the photographs. Various authors (Wagener, Krause, Kölliker, van Gehuchten), as before said, have described a fibrillation of the sarcostyles of the wing-muscles; or at least a longitudinal striation of the sarcous elements, with a dotted appearance of the transverse membranes. This striation is very plain in several of those wing-sarcostyles which are here photographed, and also in all others which are similarly prepared. It is even plainer under the microscope than in the photographs, because the mass of red-stained substance which forms the sarcous elements allows hardly any actinic light to reach the photographic plate, and the sarcous elements, when well stained, look, therefore, nearly uniformly black on the positive. It is very difficult, however, to trace the longitudinal striations

through the clear intervals under the microscope, and I was at first disposed to believe that it was confined to the sarcous elements. But the first photograph which was taken showed faintly, but unmistakably, that it extended also through those intervals. This can also be detected at certain parts of those photographs which are here reproduced. The longitudinal striation, therefore, although by far the most marked in the sarcous elements, extends through the whole length of the sarcostyle. It might, therefore, be supposed to represent a fibrillation of the sarcostyle, and this is the view which has been taken by all previous authors who have noticed the appearance. They have supposed the muscle-column to be constituted of a number of juxtaposed fibrils, each of which is composed of successive alternations of the substance composing the sarcostyle, each one, therefore, being composed, in the middle of each segment, of a rod-like portion of the sarcous element; at either end of this, and continuous with it, of a portion of the substance of the clear interval; and, lastly, at the ends of the segments, of a portion of the transverse membrane. The sarcous element is, according to this view, formed by the juxtaposition of a number of rod-like elements, which are stained by hæmatoxylin and similar methods (amongst which must be reckoned this alcohol-gold method); the clear intervals being formed of continuations of these rod-like elements, which are, however, of a different chemical nature since they do not take these stains, and exhibit different optical properties; and the transverse membranes of minute, dot-like elements having, again, different chemical and optical properties from the other parts. (The accessory disks, since they are inconstant, may, in this brief preliminary communication, be left out of account.) But the optical sections of the sarcostyles (figs. 6, 7*a*, 8, and 8*a*), *i.e.*, more especially of their sarcous elements, which, in teased preparations of muscles prepared by the alcohol-gold method, are frequently set free in the preparation, and are seen lying, as often as not, upon one surface, show conclusively that the above supposition regarding the fibrillar constitution of the sarcostyles is entirely erroneous. The sarcous elements are not made up of a bundle of rods, but are formed of a continuous substance (*sarcous substance*), staining with hæmatoxylin and with gold after hardening in alcohol, which substance is pierced by tubular canals which open at each end of the sarcous element, and in its middle abut against one another at the plane of Hensen's line. The optical section of each sarcous element shows a dozen or more of such canals, and the contents of these canals are, to all appearance, freely continuous with the transparent, colourless substance of the clear intervals; this can be made out in the longitudinal views. The longitudinal striation of the sarcous element is due to this canalisation; that of the clear interval to a prolongation of delicate lines (which may, perhaps, represent

thin septa) of the sarcous substance through the clear interval to the transverse membranes. The whole sarcostyle appears to be itself enclosed by a membrane of extreme delicacy.

If we assume, as is to all appearance the case, that the substance of the clear interval is of a fluid or semi-fluid nature, the above view of the constitution of the sarcostyle, which is illustrated with unmistakable clearness in the photographs, enables one to form a tolerably reasonable idea as to the physical change which may occur when the sarcostyle passes from the condition of extension to that of retraction, and *vice versâ*. For if the sarcostyle be extended, the sarcous elements being narrowed and laterally compressed by the extending force, the fluid which is contained in their canals will become squeezed out, and will pass into the clear intervals, while, at the same time, the process of extension will elongate the sarcous elements and separate them further from the transverse membranes. With further extension, a separation of the sarcous element in the middle may also occur, some of the expressed fluid passing into the interval between the two halves.*

On the other hand, when the extended sarcostyle becomes retracted (? contracted), the sarcous elements swell and the clear intervals become shortened so as eventually *almost* to disappear. This can only be effected by the absorption of the homogeneous substance of the clear intervals into the sarcous element, and in all probability it is imbibed into the canals or visible pores of the sarcous substance. The process may, in fact, be roughly compared with that which would occur with a series of pieces of sponge, placed at short intervals, in a thin-walled elastic tube filled with fluid. If the tube were extended the fluid would be squeezed out of the pores of the sponge, and would go to increase the volume of that in the intervals; on relaxing the extending force, the fluid would be re-imbibed by the sponge, and the intervals would be diminished. This comparison is not intended as an explanation of the mechanism of muscular contraction, but merely as an illustration of the physical changes which may reasonably be supposed to accompany the varying conditions of extension of the muscle.

The subject of this preliminary communication is treated of more fully in a detailed account of the structure of muscle which will shortly appear in the 'International Journal of Anatomy and Physiology.' Since, in that account, I shall have occasion to refer at

* This separation does not always occur with continued extension, for in the sarcostyle photographed in fig. 4 the sarcous elements of the extended part, although they show the effect of traction in their elongation and narrowing, are not separated and contracted in the middle, as in the sarcostyle shown in fig. 3, but are even slightly bulged at the centre. There appears, however, a slight tendency for their ends to separate as (? accessory disks).

considerable length to the views and statements of other recent writers on the same subject, and to indicate the bearings of these observations upon the wing-muscles on the more intricate subject of the structure of the leg-muscles of insects, and of the ordinary skeletal muscles of vertebrates, I have omitted such references and indications from the present notice. I may simply state, however, that for reasons which are given at length in the article above referred to, I regard the structure of the wing-muscles of insects as furnishing the key to the understanding of muscular structure in general, and I believe that it is possible to draw a comparison detail for detail between the two kinds of muscle which shows a complete correspondence in all essential particulars.

Description of the Photographs. (Plates 4 and 5.)

All the figures upon these plates are photographs of parts of sarcostyles of the wing-muscles of the common wasp, which had been prepared and stained by the method mentioned on page 281. In specimens thus prepared there is a considerable amount of variation in the degree to which the sarcostyles, and even the sarcous elements of the same sarcostyle, are swollen by the dilute formic acid, into which the muscle is placed after having been acted upon by gold chloride. This is noticeable in fig. 8, a part of which is further magnified in 8*a*, where, in the same sarcostyle, some of the sarcous elements are narrow, and others wide. The latter do not, I believe, belong to contracted or retracted portions of the sarcostyle, but are merely more swollen by the acid, probably because they happened to be less fixed, *i.e.*, coagulated by the previous treatment with alcohol and gold. It is noticeable also that these more swollen sarcous elements are fainter in the photographs; this is due to the fact that they are always of a bluish tint; whereas the less swollen sarcous elements are deep-red, and hence come out nearly black. The former, however, show the longitudinal striation, *i.e.*, canalisation, better than the latter. It must further be stated that the extension of the sarcostyles shown in fig. 8 has been produced in teasing the preparation with needles by the demi-desiccation process; it is quite different from the extension shown in figs. 3 and 4, which has been brought about in the living tissue prior to the advent of the hardening fluid. The sarcostyles represented in figs. 1 and 3, and the lower part of fig. 4, have been specially selected to illustrate the characteristic appearances of retraction (? contraction) and extension, because they were very distinctly red-stained and showed neither distortion from being swollen by acid nor dislocation from mechanical stretching after hardening; all the other sarcostyles which are shown in the photograph exhibit such distortion or dislocation to a greater or less extent.

PLATE 4.

Fig. 1. Part of a sarcostyle which has become fixed in the retracted (? contracted) condition.—Fig. 1*a*. The same, more magnified.

Fig. 2. Part of a retracted sarcostyle, showing a slight mechanical dislocation of some of the sarcous elements, which has been produced after hardening.—Fig. 2*a*. The same, more magnified.

Fig. 3. Part of an extended sarcostyle.—Fig. 3*a*. The same, more magnified.

Fig. 4. Portion of a sarcostyle, which, at one end, is much extended, at the other moderately extended, these conditions having probably been present before hardening. The middle part is somewhat dislocated, probably after hardening.—Fig. 4*a*. The same, more magnified.

PLATE 5.

Fig. 5. Parts of three moderately extended sarcostyles, with granules of the sarcoplasm lying between them.

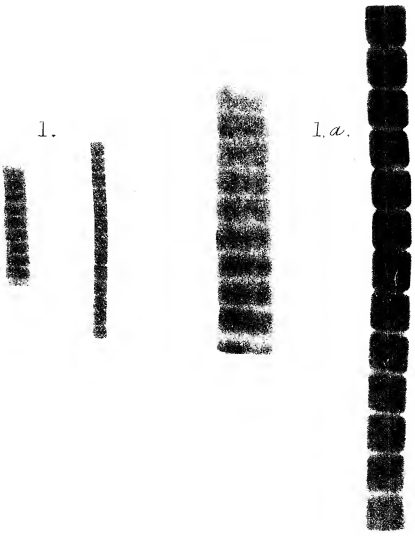
Fig. 6. Part of two adjacent sarcostyles, somewhat swollen by the formic acid. The upper terminal sarcous element of each one is swollen and flattened out, and is lying obliquely, having been probably touched by the needle in teasing the muscle. These show, especially the right-hand one, the tubular structure of the sarcous elements.

Fig. 7. Two sarcous elements lying free: one is represented in profile, the other in optical section.

Fig. 8. Photograph of part of a microscopic field, containing a number of more or less broken-up sarcostyles, and showing several of the sarcous elements lying flat, and others in profile. The tubular or canalised structure is very evident. (The globules represented are oil-drops which had accidently got into the glycerine in which the specimen was mounted.)

Fig. 8*a*. Middle part of the above photograph, enlarged; *s*, *s*, sarcous elements in profile view. Those to which the letters are adjacent show the line where separation occurs when the sarcostyle is extended (as in figs. 3 and 3*a*). Some of the other (bluer) acid-swollen elements, which come out less darkly in the photograph, exhibit the canalisation better. *s'*, *s'*, sarcous elements seen on the flat, *i.e.*, in optical section; *o*, *o*, accidental oil-globules.

Figs. 1 to 8 are photographs taken with Zeiss's 1·30 aperture, 2-mm. homogeneous achromatic objective, and with projection ocular. They are magnified 870 diameters. Figs. 1*a*, 2*a*, 3*a*, &c., are enlargements from the same negatives. They represent the tissue elements magnified 2300 diameters.


1.
1.a.

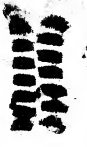

3.
3.a.


2.
2.a.


4.
4.a.

5.

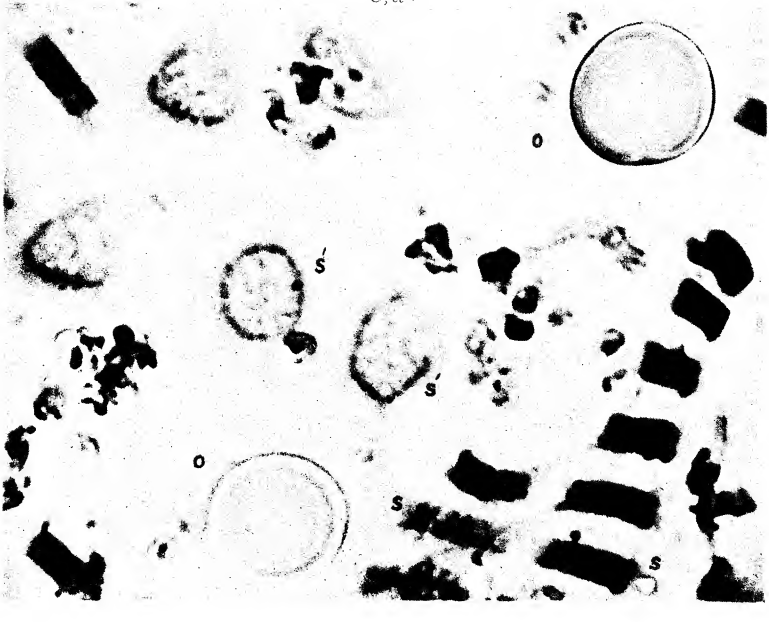
8.

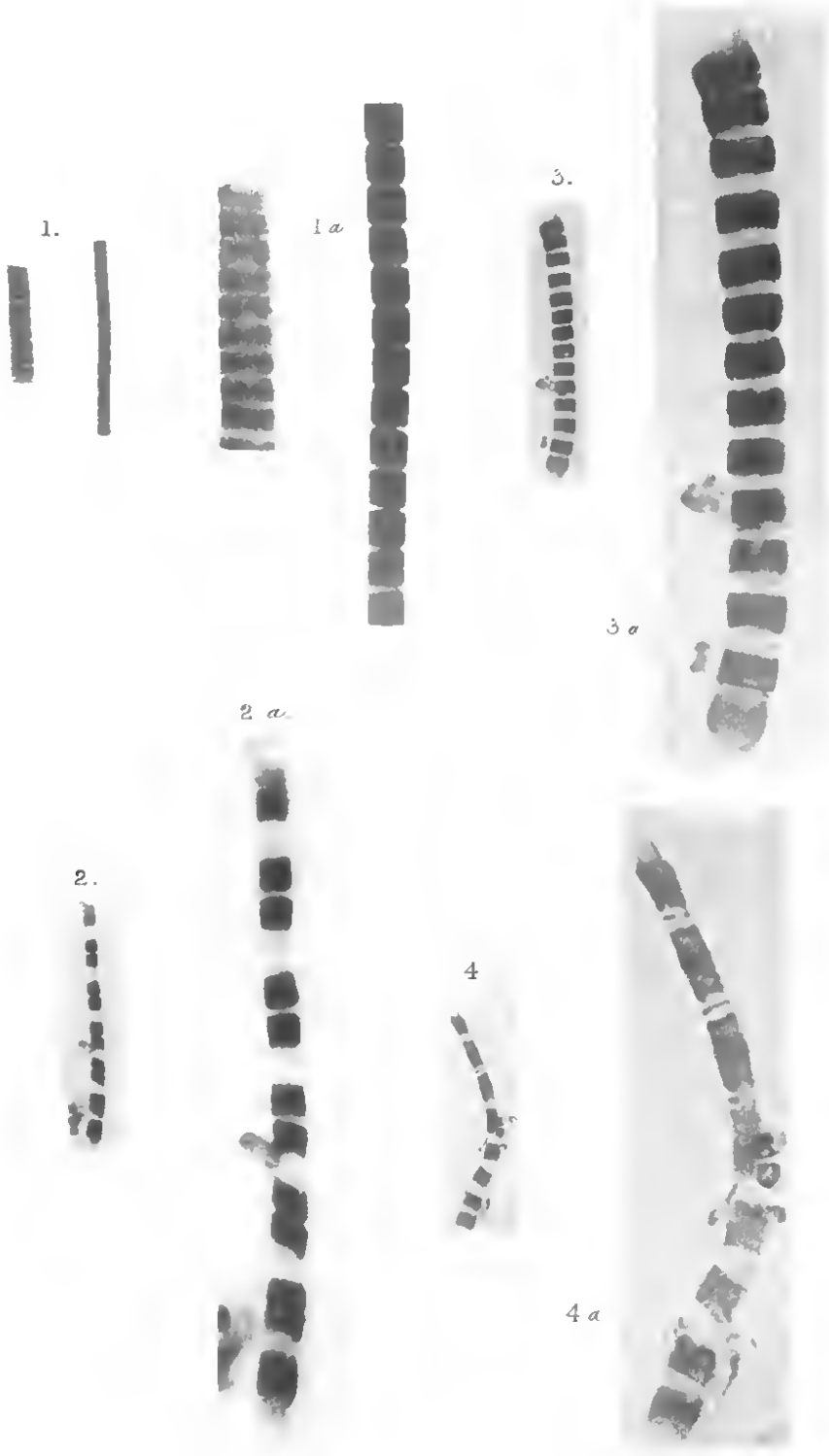


6.

7.

8, *a*.





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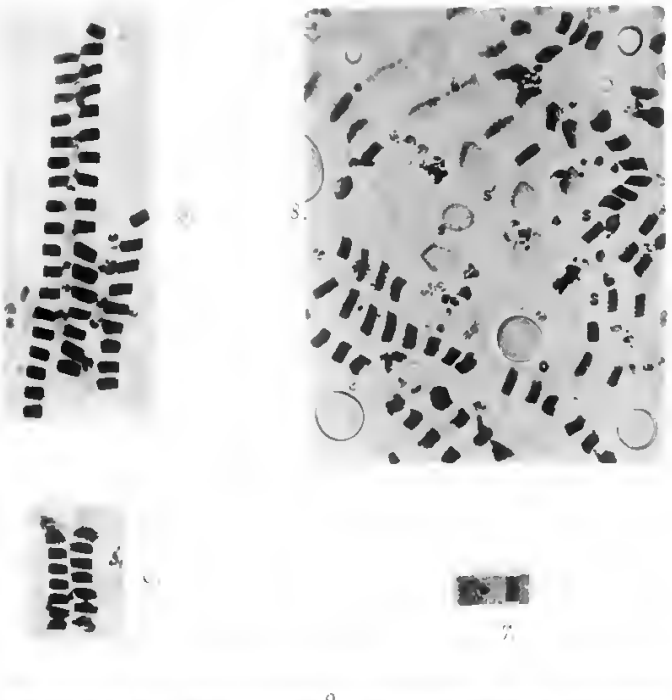
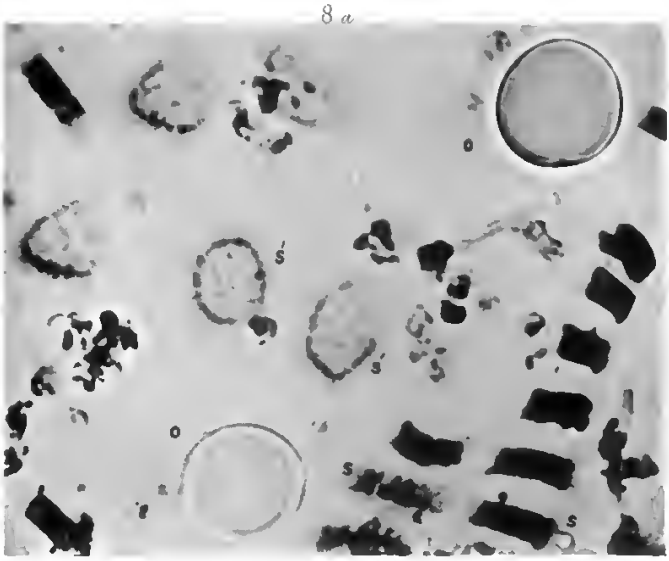


8 a



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